Patchy versus continuous distribution patterns in the African rain forest: the problem of the Anomaluridae (Mammalia: Rodentia)

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Abstract: We investigated the distribution patterns of Anomalures (scaly-tailed squirrels), a family of gliding rodents confined to African old-growth forests. The evolution of these spezialized mammals might be connected to the evolution of these forests. Current knowledge, however, does not allow conclusive confirmation of this assumption. Our analysis of both literature and specimen-based locality data has revealed two conflicting views of the distribution patterns of these animals. In most current textbooks the existence of broad continuous ranges throughout the African forest belt is postulated. By mapping actual locality data we found that patchy discontinuous distributions are equally supported. The contradictions are discussed for the respective countries in detail.

Key words: Anomaluridae, Rodentia, biogeography, African rain forest

Introduction

Anomalurids (or scaly-tailed squirrels) are highly specialized gliding rodents confined to African old-growth forests. Their existence depends on factors such as specific tree height, distance between trees and sufficient suitable tree holes. The evolution of these gliding mammals should thus be closely tied to the evolution of the African rain forest. Current knowledge, however, does not allow conclusive confirmation of this assumption.

Material and methods

For the analysis of the postulated distribution of Anomaluridae maps were taken from current textbooks (see below), enlarged to the same scale and the respective areas combined on a single map. The outlines in figs.1-3 give the maximum distribution assumed. Documented specimen-based localities were taken from various authors (see below), either redrawn from maps or from localities with given coordinates. Localities less than ca. 100 km apart were regarded as representing a continuous area and thus combined.

Distribution patterns

Our analysis of both literature and specimen-based locality data has revealed two conflicting views of the distribution patterns of these animals. In most current textbooks (McLaughlin 1984, Rahm 1988, Kingdon 1997) the existence of broad continuous distributions throughout the African forest belt is postulated (figs.1-3).

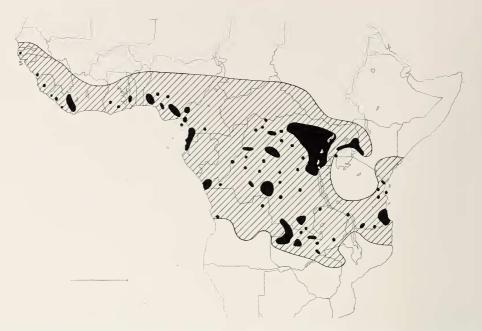


Fig.1: Presumed continuous distribution of the Anomalurinae as postulated by various authors (hatched area) contrasted with the documented localities (solid black areas); see text for references. Scale = 1000 km.



Fig.2: Presumed continuous distribution of *Idiurus* as postulated by various authors (hatched area) contrasted with the documented localities (solid black areas); see text for references. Scale = 1000 km.

By mapping actual locality data from the literature (Sanderson 1940, Rosevear 1953, Rahm 1960, Eisentraut 1963, Rahm & Christiaensen 1963, Verheyen 1963, Kuhn 1965, 1966, Rahm 1966, Rahm & Christiaensen 1966, Verheyen 1968, Jones 1971, Roche 1972, Kingdon 1974, Delany 1975, Ansell 1978, Happold 1987, Ansell & Dowsett 1988, Pérez del Val et al. 1995, Robbins & Van der Straeten 1996) and from voucher specimens we found that patchy discontinuous distributions are equally supported (figs.1-3). Our preliminary results thus suggest that the patterns of distribution in anomalurids are more complex. The discrepancy between assumed and real data differs among countries, therefore some areas will be discussed in detail in the following sections.



Fig.3: Presumed continuous distribution of *Zenkerella* as postulated by various authors (hatched area) contrasted with the documented localities (solid black areas); see text for references. Scale = 1000 km.

1. Senegal to Togo

In most current textbooks a broad belt of continuous distribution over West Africa is assumed, with a northwestern extension of Anomalurinae into The Gambia and Senegal, and an extension of *Idiurus* to Liberia. Contrary to the postulated distribution, documented localities from the western range of the Anomaluridae are extremely scattered. In most cases only a single animal was recorded, which often became the type specimen of a new taxon. Except for small clusters along the Liberia-Ivory Coast border and in Benin the specimen-based localities are usually isolated, with several hundred km distance between them. From The Gambia and Guinea-Bissau no findings are recorded.

Certainly the small number of records is partly due to the lack of expeditions to this area. But apart from this a broad continuous distribution is impossible because of the very scattered occurrence of rain forests. Particularly the postulated

distribution for *Idiurus* seems exaggerated, as it is only based on two isolated findings in Sierra Leone and Ghana.

2. Benin

Contrary to the postulated distribution of *Idiurus* and the Anomalurinae in this area no findings were recorded in the literature investigated. Analogous to the more western countries this may partly be due to the lack of collections, but in Benin the savanna extends down to the coastal region and separates the rain forest areas (Dahomey Gap: Grubb 1978, Robbins 1978), so in this country the occurrence of animals dependent on rain forest is unlikely.

3. Nigeria

This is the westernmost country with several observations of Anomalurinae, often less than one hundred km apart. Without a thorough investigation of additional material it is impossible to decide whether the gaps between the recordings are due to a lack of information or to the occurrence of an insurmountable obstacle. Despite numerous findings of Anomalurinae no *Idiurus* was recorded, which seems to indicate that the genus does not occur in this area, contrary to the postulated distribution.

4. Cameroon and Equatorial-Guinea

From these two countries findings of all groups of Anomaluridae are recorded. The distribution can be divided into several areas. Records of Anomalurinae and *Idiurus* originate from the Bambouto Mountains and the Cameroon Mountain in western Cameroon. The nearest findings to these are separated by a gap of some two hundred km and lie in southwestern Cameroon and western Equatorial Guinea and include Anomalurinae, *Idiurus* and *Zenkerella*. The island of Bioko is inhabited by at least two members of the Anomalurinae and *Zenkerella*, but no *Idiurus* is documented. From the center and east of southern Cameroon only a few scattered findings, mainly of *Zenkerella*, are recorded.

5. Gaboon, Congo and Central African Republic

In these countries the records are very rare and scattered, with findings of Anomalurinae near the northern coastal area of Gaboon and three widely separated localities for *Zenkerella*, two in Congo and one in the Central African Republic. Obviously the southern extent of the distribution of *Idiurus* and *Zenkerella* in Gaboon has been overestimated.

6. Democratic Republic of Congo and Cabinda

The records from this area are the most evenly distributed, at least for the Anomalurinae. From Cabinda and the extreme west of the Democratic Republic of Congo, between Popular Republic of Congo and Angola, several localities have been recorded, separated from the rest by a gap of some three hundred km.

The distribution of Anomalurinae in the main part of the Democratic Republic of Congo is difficult to interpret, because on the one hand the localities are very evenly distributed and on the other hand they show an average inter-locality distance of 100-150 km. As in the case of Nigeria, a better interpretation of the distribution pattern in the central Democratic Republic of Congo would require more information about these localities.

A different situation is found in the northeast of the country, where documented localities of Anomalurinae are usually less than 100 km apart. In this area a continuous distribution is very likely. The *Idiurus* records are more scattered, but an area that supports a continuous distribution of Anomalurinae may also provide suitable habitats for *Idiurus*. However a connection between the *Idiurus* population in the Congo Basin and that in West Africa, as postulated in the literature, is extremely unlikely. Although the region between the two areas was thoroughly investigated, no specimens were recorded; therefore the *Idiurus* population of the Congo Basin must be regarded as geographically separate from the population in Cameroon.

7. Angola

From Angola only two isolated findings are reported in the literature studied. Because it is mainly gallery forest that is available for anomalurids in this country, localities that do not belong to the same river system must be regarded as separated from one another.

8. Zambia

In western Zambia the situation is similar to Nigeria and central Congo: numerous records, some in clusters and obviously belonging to a continuous distribution, gaps of about 150 km between clusters, and also some isolated findings. No records are known from the southern part of Zambia, and only two isolated findings from the eastern part.

9. Rwanda and Burundi

From each of these countries a single finding is recorded. The locality in Rwanda is probably connected with the Anomalurinae distribution in Uganda, since the distance to the nearest locality there is just about 100 km.

10. Uganda and Kenya

The distribution in Uganda seems to be divided into two parts: the recorded localities near the border to the Democratic Republic of Congo very likely belong to the Anomalurinae area in northeastern Congo. Clearly separated from this area are the localities north of Lake Victoria in Uganda and Kenya.

11. Tanzania and Malawi

The Anomalurinae in Tanzania are separated from the populations of Kenya in the north and Zambia in the south respectively by gaps of more than 500 km, so a connection is very unlikely. Only one locality is known from Malawi.

Systematics

At present the 39 described taxa of the Anomaluridae are grouped into seven species (table 1). Our preliminary data, however, suggest that the taxon diversity has been underestimated. Some taxon names, such as the genus *Anomalurops* Matschie, 1914, will have to be resurrected.

Table 1: Concepts of the number of genera, species and subspecies of Anomaluridae from 1897 to 1997

Author	no of genera	no of species	no of subspecies
Trouessart 1897	2	10	
Allen 1939	5	17	29
Ellerman 1940	4	9	25
Malbrant & Maclatchy 1949	5	8	10
Grassé & Dekeyser 1955	4	7	_
Rosevear 1969	4	7	15
Misonne 1971	3	7	
Rahm 1988	3	7	20
Dieterlen 1993	3	7	_
Starck 1995	3	9	-
Kingdon 1997	3	7	

Conclusions

The level of discrepancy between assumed and documented distributions differs between countries, but generally the presumed area appears to be an overestimate. Particularly the northern distribution of the Anomalurinae and the southern range of *Idiurus* and *Zenkerella* are not supported by recorded findings. In addition, well-known rain forest clearings such as the Dahomey Gap in Benin are often ignored. Sometimes all recorded localities of a taxon are presumed to belong to one continuous distribution area, even in cases where no findings were documented for some 1500 km, as in the genus *Idiurus*.

The analysis of distribution patterns in this group is also complicated by the lack of information due to the low level of zoological exploration of some areas, particularly in West Africa. For Nigeria, Cameroon and the Congo Basin countries, data from already existing museum specimens may solve some of the problems. Such data may support either separated clusters with clearly defined gaps or continuous distributions.

Another source of confusion regarding the distributions of the Anomaluridae is the controversial taxonomy of the group. It is sometimes impossible to tell which species (or even genus) an author refers to in a publication dealing with locality records.

Our further research will thus focus on the taxonomy and phylogeny of this interesting group of mammals in order to answer some of the questions encountered, particulary concerning their phylogeography.

References

- Allen, G. M. (1939): A checklist of African Mammals. Bull. Mus. Comp. Zool. Harvard College 83: 1-763.
- Ansell, W.F.H. (1978): The Mammals of Zambia. The National Parks & Wildlife Service, Chilanga, Zambia.
- Ansell, W.F.H. & R.J. Dowsett (1988): Mammals of Malawi. The Trendrine Press, Zennor, U.K.
- Delany, M.J. (1975): The Rodents of Uganda. Trustees of the British Museum (Natural History), London.
- Dieterlen, F. (1993): Family Anomaluridae. –pp.757-758 in: Mammal Species of the World. A taxonomic and geographic reference. 2nd edition (eds. Don E. Wilson & DeeAnn M. Reeder). Smithsonian Institution Press, Washington, London.
- Eisentraut, M. (1963): Die Wirbeltiere des Kamerungebirges unter besonderer Berücksichtigung des Faunenwechsels in den verschiedenen Höhenstufen. Paul Parey, Hamburg & Berlin.
- Ellerman, J.R. (1940): The families and genera of living rodents. Volume I: Rodents other than Muridae. British Museum (Natural History), London.
- Grassé, P.P. & P.L. Dekeyser (1955): Ordre des Rongeurs. pp. 1321-1525 in: Traité de Zoologie. Anatomie, Systematique, Biologie. (ed. Pierre P.Grassé). 17, 2, Paris.
- Grubb, P. (1978): Patterns of speciation in African mammals. Bull. Carneg. Mus. nat. Hist. 6: 152-167.
- Happold, D.C.D. (1987): The mammals of Nigeria. Clarendon Press, Oxford.
- Jones, C. (1971): Notes on the anomalurids of Rio Muni and adjacent areas. J. Mammal. 52: 568-572.
- Kingdon, J. (1974): East African mammals. An Atlas of Evolution in Africa. Volume II Part B (Hares and Rodents). Academic Press, London, New York.
- Kingdon, J. (1997): The Kingdon Field Guide to African Mammals. Academic Press, London.
- Kuhn, H.-J. (1965): A provisional check-list of the mammals of Liberia. Senckenbergiana biol. 46: 321-340.
- Kuhn, H.-J. (1966): Anomalurus pelii auzembergeri in Liberia. J. Mammal. 47: 334-338.
- Malbrant, R. & A. Maclatchy (1949): Faune de l'Équateur Africain Français. Tome 2. Mammifères. Encyclopédie biologique 36. Lechevalier, Paris.
- McLaughlin, C.A. (1984): Protogomorph, Sciuromorph, Castorimorph, Myomorph (Geomyid, Anomalurid, Pedetoid, and Ctenodactyloid) Rodents. pp. 267-288 in: Orders and families of recent mammals of the world (eds. S. Anderson & J. Knox Jones Jr.). John Wiley & Sons, New York: 267-288.
- Misonne, X. (1971): Rodentia. pp. 1-39 in: The Mammals of Africa. An identification Manual (eds. J. Meester & H.W. Setzer). Smithsonian Institution Press, City of Washington.

- Pérez del Val, J., J. Juste & J. Castroviejo (1995): A review of Zenkerella insignis Matschie, 1898 (Rodentia, Anomaluridae). First records in Bioko island (Equatorial Guinea). – Mammalia 59: 441-443.
- Rahm, U. (1960): L' *Anomalurus jacksoni* de Winton: Répartition, biologie et observations en captivité. Bull. Soc. Roy. Zool. Anvers 18: 3-13.
- Rahm, U. (1966): Les mammifères de la forêt équatoriale de l'Est du Congo. Ann. Mus. Roy. Afr. Centr. 149: 39-121.
- Rahm, U. (1988): Dornschwanzhörnchenverwandte. pp. 116-125 in: Grzimeks Enzyklopädie Säugetiere (ed. B. Grzimek). Kindler Verlag, München, Band 3.
- Rahm, U. & A. Christiaensen (1963): Les mammifères de la région occidentale du lac Kivu. Ann. Mus. Roy. Afr. Centr. 118: 1-83.
- Rahm, U. & A. Christiaensen (1966): Les mammifères de l'île Idjwi (Lac Kivu, Congo). Ann. Mus. Roy. Afr. Centr. 149: 1-35.
- Robbins, C.B. (1978): The Dahomey Gap a reevaluation of its significance as a faunal barrier to West African high forest mammals. Bull. Carneg. Mus. nat. Hist. 6: 168-174.
- Robbins, C.B. & E. Van der Straeten (1996): Small mammals of Togo and Benin. Mammalia 60: 231-242.
- Roche, J. (1972): Capture de Zenkerella insignis (Rongeurs, Anomaluridés) en République Centrafricaine. Mammalia 36: 305-306.
- Rosevear, D.R. (1953): Checklist and Atlas of Nigerian Mammals with a foreword on Vegetation. F. Howard Doulton & Co., London.
- Rosevear, D.R. (1969): The rodents of West Africa. British Museum (Natural History), London.
- Sanderson, I.T. (1940): The mammals of the North Cameroons forest area. Trans. Zool. Soc. Lond. 24: 623-725.
- Starck, D. (1995): Lehrbuch der speziellen Zoologie. Band 2, Teil 5/2: Säugetiere. Gustav Fischer Verlag Jena.
- Trouessart, E.-L. (1897): Catalogus Mammalium tam viventium quam fossilium. Fasciculus I. Berolini, R. Friedländer & Sohn.
- Verheyen, W.N. (1963): Contribution à la systématique du genre *Idiurus* (Rodentia-Anomaluridae). Rev. Zool. Bot. Afr. 68: 157-197.
- Verheyen, W.N. (1968): The Anomalurinae of the Congo (Rodentia: Anomaluridae). Rev. Zool. Bot. Afr. 77: 392-411.

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